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THE HEART VALVES OF THE ELASMOBRANCH FISHES

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The heart valves of the elasmobranch fishes have been the subject of discussion from time to time and have been somewhat extensively described by Garman (1913). During my investigations leading to the classification of the elasmobranch fishes recently published (see American Museum Novitates No. 837) a great many heart valves were examined, and, since my conclusions do not entirely agree with those of previous investigators, the results are presented at this time.

The material used in this work has been collected over a series of years, and I am indebted to the following scientists and institutions for material and research facilities:

To Dr. W. K. Gregory and his associates of the Department of Ichthyology at The American Museum of Natural History in New York City for the use of material and research facilities at the Museum.

To Dr. Naohide Yatsu, to Dr. Negumi Eri, and to Dr. Shigeho Tanaka for access to valuable material and for research facilities at the Imperial University at Tokyo, and at the Marine Biological Laboratory at Misaki, Japan. Also to the old collector, Kuma Aoki, of the Laboratory for a specimen of the rare *Chlamydoselachus anguineus*.

To Dr. H. C. Delsman, and his associates at the Laboratorium voor Het, Onderzoek der Zee, Batavia, Java, for access to material, and research facilities at the laboratory.

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As far as possible direct examination of the hearts has been made, but in cases where comparisons were necessary, and specimens not available, figures have been redrawn from the literature. The terminology used is that of my recent classification mentioned above.

In all fishes the conus arteriosus of the heart is functional and contains a varying number of valves. In the higher Osteopterygia there is a separation between the two regions of the conus, the anterior portion being strengthened, and the valves restricted to a single row in the

posterior portion. In the lower Osteopterygia, and in the elasmobranchs, there is no such division, the entire conus being valvular. The development within the elasmobranchs, therefore, does not parallel that of the typical fishes, but the conditions found in the lower Osteopterygia (see *Ceratodus forsteri*, Fig. 1i) is reminiscent of some of the higher elasmobranchs, and may be the continuation of a process begun in the lower group.

In the elasmobranchs the number of valves varies from three series of valves in two rows, as found in the Orectoloboidea, to four series in five rows in the Hexanchea, and six or seven rows in some of the rays. Although variation occurs even between members of the same species, still it tends to fall within limits characteristic of a group, or to show transitional stages toward a higher group, and for that reason the heart valves may be used as one of the contributing characters in establishing a classification.

The question is whether the small number or the large number is primitive. Garman (1885) suggests that the large number is primitive, and that reduction has occurred in the elasmobranchs with the increase of specialization. He admits, however, that the opposite appears to be true in the rays. Lankester (1878) suggests that duplication occurs in some cases in a longitudinal direction.

In the opinion of the author the tendency in the elasmobranchs is for duplication of valves rather than reduction, and this duplication may take place transversely as well as longitudinally. In some cases valves arising by longitudinal division in one row may be pushed downward, and thus give rise to an additional row.

Table I gives a graphic picture of my theory of relationships among the elasmobranch fishes based on the heart valves. Tables II, III, and IV show the number of rows found in specimens examined by dissection or described in the literature. Illustrations of all types, though not of all species, will be found in the figures. Where no reference is given the material has been dissected by the author and drawn direct from the specimen.

In the Hexanchea the tendency is for a large number of valves, usually in four series of four or five rows. Garman's figure of *Heptranchias perlo* shows three series of five rows, the row directly beneath the membranous valves being very minute. In 1885, Garman quoted Owen as saying that both *Hexanchus* and *Heptranchias* have four rows of valves. He himself describes two species, a young *Notorhynchus pectorosus* (*Heptranchias*) with five rows, and a large *Heptranchias*

maculatus with only three rows, but with traces in the middle of the conus as of two rows which he calls obsolete.

I find a mature specimen of *Notorhynchus pectorosus* with only four rows, but in four series which would seem to indicate duplication rather than reduction (Fig. 1a). A specimen of *Chlamydoselachus* shows four distinct series with five rows; the fourth row is in the process of duplication (Fig. 1d). This varies considerably from Garman's figure (1885) in which he shows only three series of valves. The fourth series has been found in no other group of the elasmobranchs but is frequently found in the Osteopterygia (Fig. 1i).

The valves of *Chlamydoselachus* are more membranous than those of other types, but there is a general resemblance between them. The conus is long, and the upper row of valves is membranous in all. The valves extend down by a chord to the lower row, some of which have thickened walls. A distinct tendency to duplication is apparent in all members of the order, and it is reasonable to look upon Garman's vestigial fifth row as a rudimentary fifth in *Heptanchias*.

On the theory of duplication it will be apparent that the Hexanchea have exceeded the usual speed of development. This is not unexpected, however, since it is a well-known fact that this group is highly specialized in certain characters while retaining others in archaic condition. This duplication is paralleled, also, in the spiral valves and in the gill openings.

The same appears to be true in the Odontaspoidea, another group with some archaic characters. In a specimen of *Scapanorhynchus owstoni* examined by the author (Fig. 1g) the valves do not differ from the one figured by Garman in 1913. It is clear that duplication in the transverse direction is in progress, for the chordae tendineae in the upper row of valves mark off a decidedly thickened area at the base of the membranous valves. These have not yet separated off, as no cleavage of the tissue has taken place. The same condition is found in a young specimen of *Carcharias taurus* (Fig. 1f) except that here the duplication is occurring in the second instead of the first row of valves. In both species the conus is shorter than in the Hexanchea.

Two rows are characteristic of the Holocephali, the Orectoloboidea, and the Catuloidea, but are the exception in other groups. Three rows are characteristic of the Odontaspoidea, although duplication is in progress. Three rows are also characteristic of the Carcharinoidea and of the Isuroidea. The only tendency to duplication in either of these groups is found in one species of the Galeorhinidae. The Isuridae, Carcharinidae, and Sphyrnidae are apparently well-stabilized groups.

One of the most interesting types found was *Catulus torazame* (Fig. 9d). The heart was taken from a mature female with complete egg cases in the oviduct and is not, therefore, in a transitional stage in the life of the individual. There is an obvious transverse duplication in progress here, and, since the typical number for the group is two rows, this bears out my conclusion that *Catulus torazame* is a transitional type approaching the stable condition prevailing throughout the Carcharinoidea.

In *Calliscyllium venustum* (Fig. 9b) three rows are already established in a group in which two rows are typical. This species also shows other transitional characters bridging the gap between *Catulus torazame* and the Carcharinoidea.

The recent acquisition of the heart of a thirty-foot whale shark, *Rhineodon typus* (Fig. 5), gives an interesting picture of duplication in progress. Here there are two definite rows, the upper membranous and the lower row attached to the upper by chords. Additional pockets are formed on some of the lower valves and between them are two completely formed additional valves. These represent longitudinal multiplication and if later pushed down would form a third row.

Rhineodon is a highly specialized shark and externally it possesses such mixed characters that its classification has long been a matter of doubt. In 1930 I described the teeth, denticles, claspers, vertebrae, and certain of the jaw parts and from the combined evidence decided that this shark was a specialized isuroid. The valves of the heart, however, suggest relationship to the lower group, Orectoloboidea. Duplication is more often found in the lower groups, also, since they are frequently in a varying condition with tendencies approaching higher groups. *Rhineodon* is too specialized to be considered in any way transitional, but the duplication is doubtless an expression of this specialization.

The Heterodontea and the Chismopneae have both typically two rows although three occur in some specimens of *Chimaera*. These are groups of low development and ancient origin.

The Squalae show variable tendencies even within the species, *Squalus acanthias* (Figs. 3a and 3c) having two rows in some specimens and three in others. This is unusual and may indicate a mutating species. Other species of *Squalus* (Fig. 3g) and *Etmopterus* (Fig. 3e) have four rows, which give the group a most unstable appearance. This is paralleled in other characters and is doubtless an indication of their transitional character.

The Platosomeae and quite possibly the Galea had their origin in the ancestral squaloids. The Platosomeae show extreme duplication of the heart valves reaching six and even occasionally seven rows (Fig. 12).

The condition commonly found among the lower Osteopterygia, and shown by *Ceratodus forsteri* (Fig. 1i) may well be carrying on a condition of duplication already well under way among the elasmobranchs.

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TABLE I.—Groups arranged to show relationships based on the number of rows of valves in the bulb. Genera showing transitional conditions are shown in smaller type. In this characteristic the Hexanchea and the Carcharioidea have shown extreme specialization.

Heart Valves in		Rows	
5-7 Rows		4-5 Rows	
Plotosomæ		Hexanchæ	
Squalæ		3-4 Rows	Odontaspidoidea
		3 Rows	Isuroidea
Squalus		2-3 Rows	Galeorhinus
			Carcharioidea
Holocephali		2 Rows	Calliscyllium
			Catulus
Squalus		2 Rows	Orectoloboidea
			Catuloidea

TABLE II.—Heart Valves.

	NUMBER OF ROWS
CHISMOPNEAE	
<i>Callorhynchus callorhynchus</i> (Fig. 2d)	2
<i>Chimaera monstrosa</i> (Goodrich)	2
(Lankester) (Fig. 2e)	3
ANTACEAE	
Heterodontea	
<i>Heterodontus japonicus</i> (Fig. 2a)	2
Squalea	
<i>Squalus acanthias</i> (Fig. 3c)	2
(Fig. 3a)	3
<i>Pristiophorus japonicus</i> (Garman)	3
<i>Squalus fernandinus</i> (Fig. 3g)	4
<i>Etmopterus lucifer</i> (Fig. 3e)	4
PLATOSOMEAE	
Narcobatoidea	
<i>Narke japonica</i> (Garman)	2
<i>Narcacion marmoratum</i> (Garman)	3
Rhinobatoidea	
<i>Rhinobatus percellens</i> (Garman)	4
<i>Discobatus sinensis</i> (Garman)	4
Dasybatoidea	
<i>Discus thayeri</i> (Garman)	4
<i>Pteroplatea altavela</i> (Garman)	5
<i>Aetobatus narinari</i> (Garman) (Fig. 12a)	5
<i>Mobula hypostoma</i> (Garman) (Fig. 12f)	6
<i>Rhinoptera jussieu</i> (Garman) (Fig. 12c)	7

TABLE III.—Heart Valves.

	NUMBER OF ROWS
ANTACEAE	
Galea	
Orectoloboidea	
<i>Orectolobus japonicus</i> (Garman) (Fig. 4f)	2
<i>Chiloscyllium griseum</i> (Fig. 4e)	2
<i>Chiloscyllium indicum</i> (Fig. 4g)	2
<i>Chiloscyllium plagiosum</i> (Fig. 4a)	2
<i>Stegostoma tigrinum</i> (Fig. 4b)	2
<i>Rhineodon typus</i> (Fig. 5)	2
Odontaspoidea	
<i>Carcharias taurus</i> (Fig. 1f)	3
<i>Scapanorhynchus owstoni</i> (Fig. 1g)	3
Isuroidea	
<i>Isurus punctatus</i> (Garman) (Fig. 7c)	3
<i>Carcharodon carcharias</i> (Parker) (Fig. 7f)	3
<i>Vulpecula marina</i> (Goodrich)	3
Hexanchea	
<i>Hexanchus</i> (Owen)	4
<i>Heptranchias perlo</i> (Garman)	4
<i>Notorhynchus pectorosus</i> (Garman) (Fig. 1a)	4
	5
<i>Heptranchias maculatus</i> (Garman)	5
<i>Chlamydoselachus anguineus</i> (Garman)	4
(Fig. 1d)	5

TABLE IV.—Heart Valves.

		NUMBER OF ROWS
ANTACEA		
Galea		
Catuloidea		
<i>Halaelurus burgeri</i> (Fig. 8f)	2	
<i>Halaelurus bivius</i> (Fig. 8a)	2	
<i>Parmaturus xaniurus</i> (Fig. 9f)	2	
<i>Pristiurus eastmani</i> (Fig. 8d)	2	
<i>Cephaloscyllium umbratile</i> (Garman)	2	
<i>Atelomycterus marmoratus</i> (Fig. 8b)	2	
<i>Catulus retifer</i> (Fig. 9a)	2	
<i>Catulus torazame</i> (Fig. 9d)		3
<i>Calliscyllium venustum</i> (Fig. 9b)		3
Carcharinoidea		
<i>Triakis scyllium</i>		3
<i>Galeorhinus mustelus</i> (Fig. 10b)		3
<i>Galeorhinus laevis</i> (Fig. 10a)		3
<i>Galeorhinus fasciatus</i> (Fig. 10e)		3
<i>Galeorhinus manazo</i> (Fig. 10d)		4
<i>Galeus glauca</i> (Fig. 7d)	2	
<i>Eugaleus galeus</i> (Fig. 7a)		3
<i>Carcharinus sorrah</i> (Fig. 11d)		3
<i>Carcharinus porosus</i>		3
<i>Carcharinus commersonii</i> (Fig. 11e)		3
<i>Carcharinus milberti</i> (Fig. 11a)		3
<i>Carcharinus acronotus</i>		3
<i>Carcharinus spallanzani</i>		3
<i>Scoliodon wahlbeehmi</i>		3
<i>Physodon mülleri</i>		3
<i>Sphyrna zygaena</i> (Fig. 11c)		3
<i>Sphyrna blochii</i> (Fig. 11g)		3

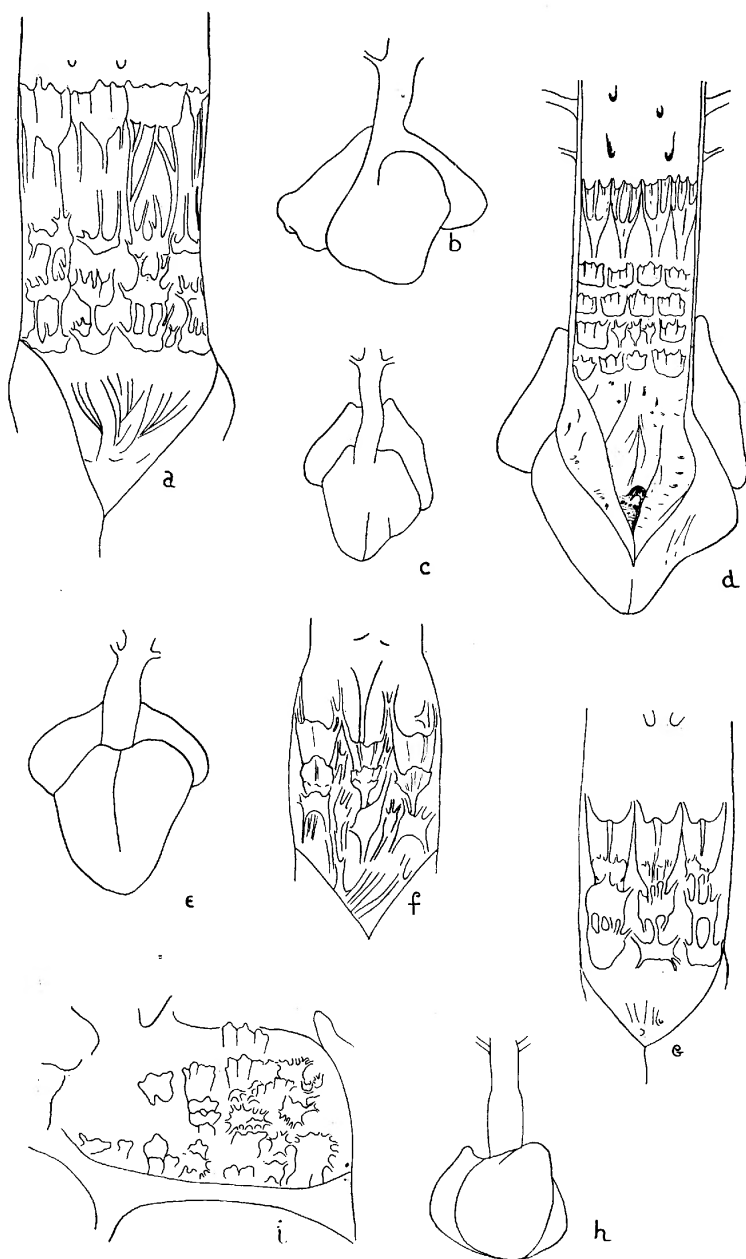


Fig. 1. Hearts and heart valves in the open conus. Note transverse duplication in *f*, *g*, and *i*; and longitudinal duplication in *a* and *d*.

a and *b*, *Notorhynchus pectorosus*; *c* and *d*, *Chlamydoselachus anguineus*; *e* and *f*, *Carcharias taurus*; *g* and *h*, *Scapanorhynchus owstoni*; *i*, *Ceratodus forsteri*, after Lankester.

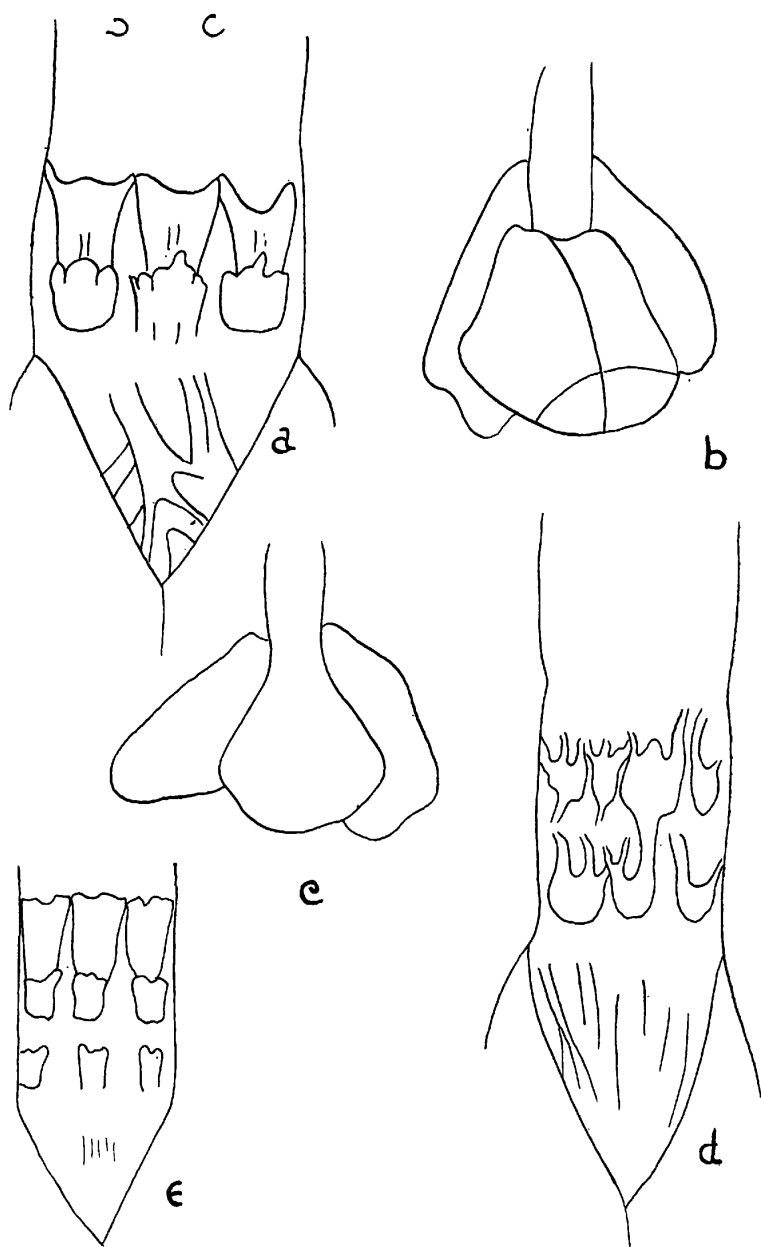


Fig. 2. Hearts and heart valves in the open conus. Note longitudinal duplication in the upper row of *d*.

a and *b*, *Heterodontus japonicus*; *c* and *d*, *Callorhynchus callorhynchus*; *e*, *Chimaera monstrosa*, after Lankester.

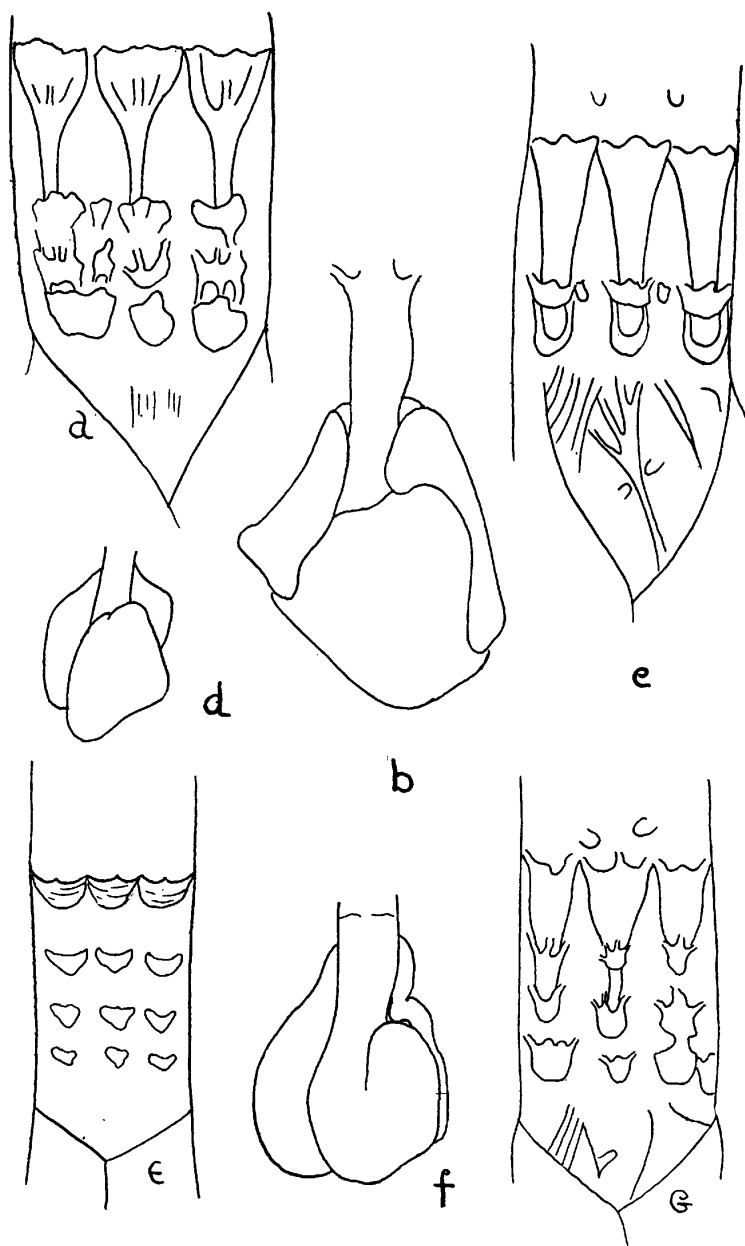


Fig. 3. Hearts and heart valves in the open conus. Note variation in *Squalus acanthias*, and longitudinal duplication in a, c, and g.

a, *Squalus acanthias*, north Atlantic specimen; b, *Squalus fernandinus*; c, *Squalus acanthias*, South American specimen; d and e, *Etmopterus lucifer*; f, *Squalus acanthias*, north Atlantic specimen; g, *Squalus fernandinus*.

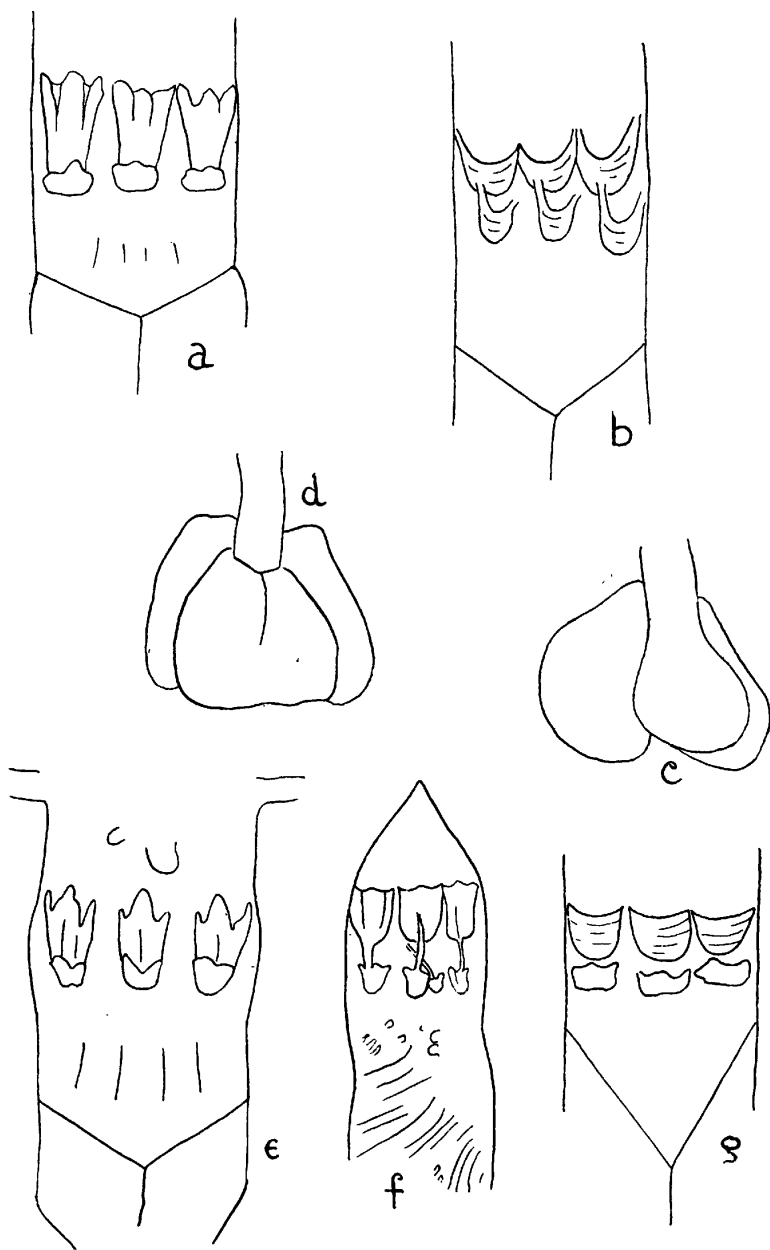


Fig. 4. Hearts and heart valves in the open conus.

a, *Chiloscyllium plagiosum*; b and c, *Stegostoma tigrinum*; d and e, *Chiloscyllium griseum*; f, *Orectolobus japonicus*, after Garman; g, *Chiloscyllium indicum*.



Fig. 5. Conus of heart of *Rhineodon typus*, drawn from fresh specimen. Width of conus opened, 16 inches.

u, upper row of valves; *l*, lower row of valves; *a*, accessory valve.

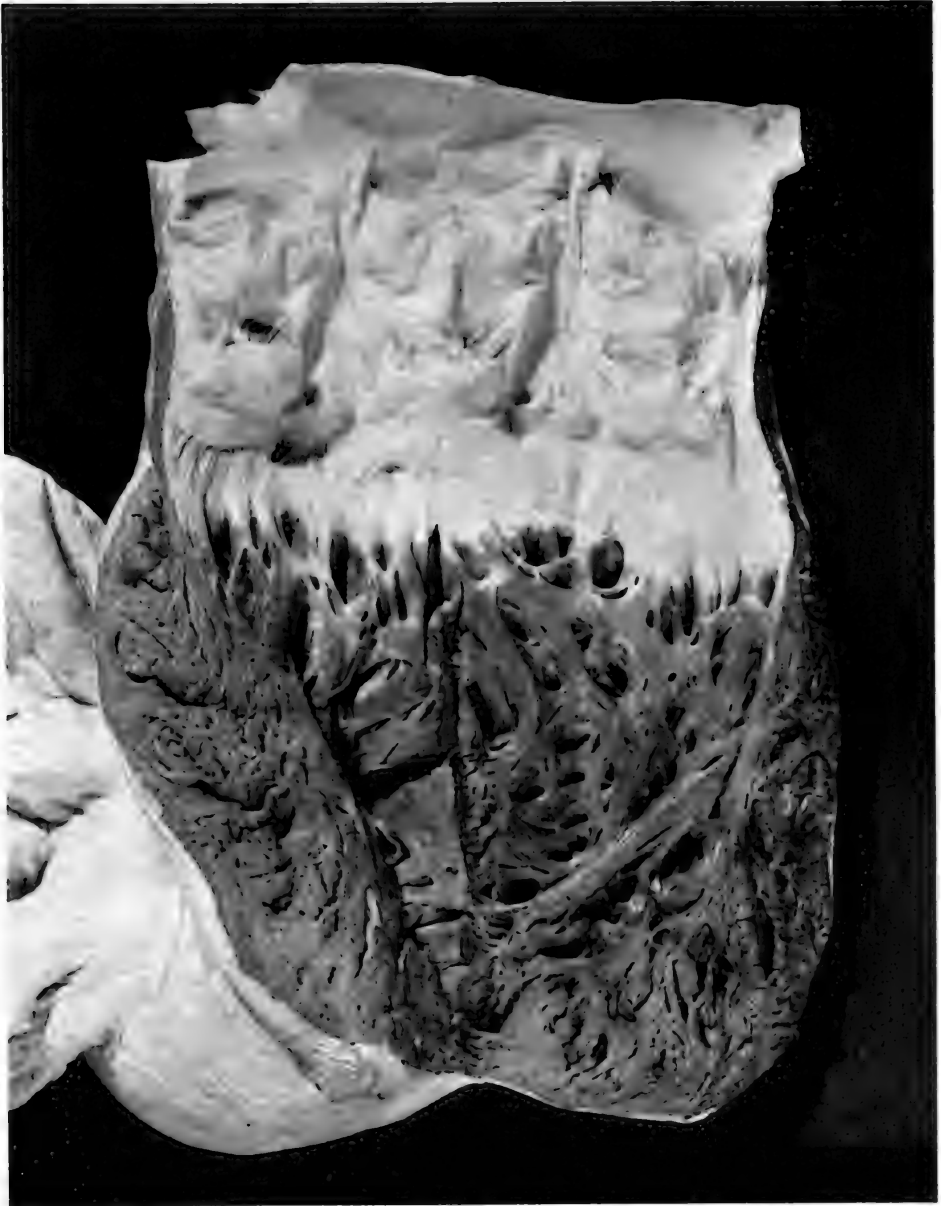


Fig. 6. Photograph of heart of *Rhineodon typus*, open to show valves.

Photograph by A. M. N. H.

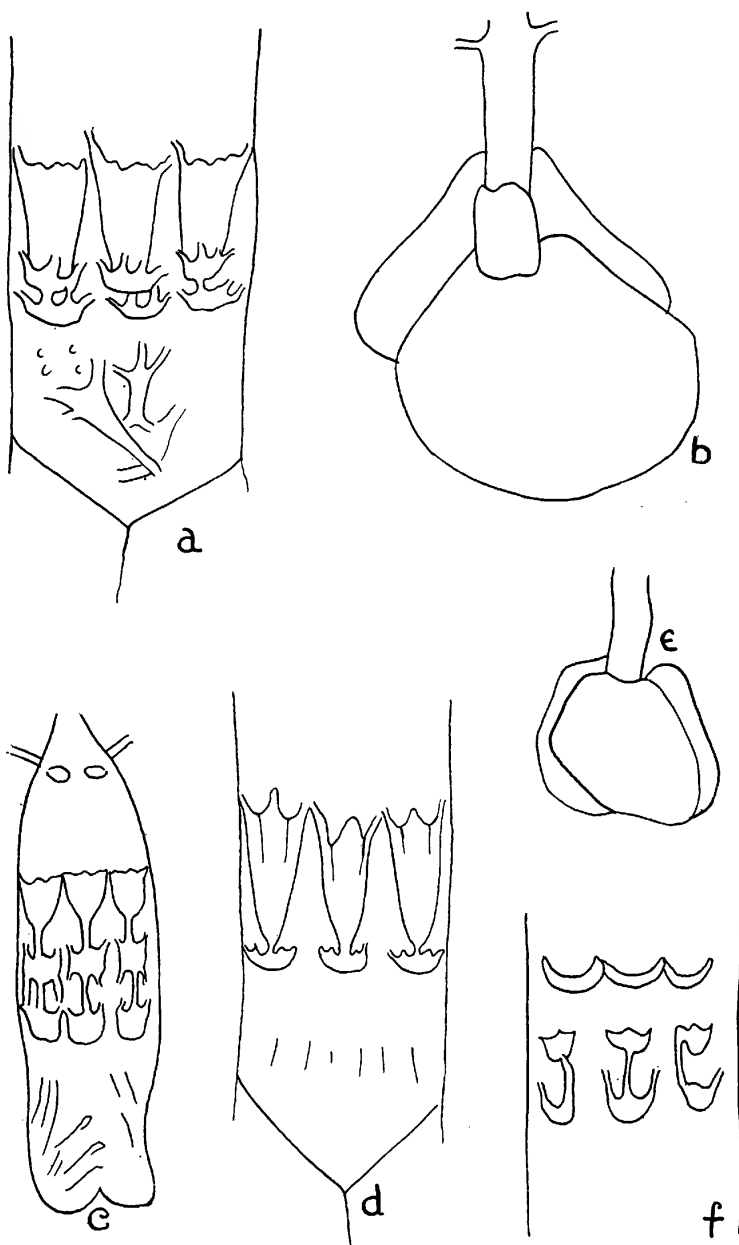


Fig. 7. Hearts and heart valves in the open conus.
a and *b*, *Eugaleus galeus*; *c*, *Isurus punctatus*, after Garman; *d* and *e*, *Galeus glauca*; *f*, *Carcharodon carcharias*, after Parker.

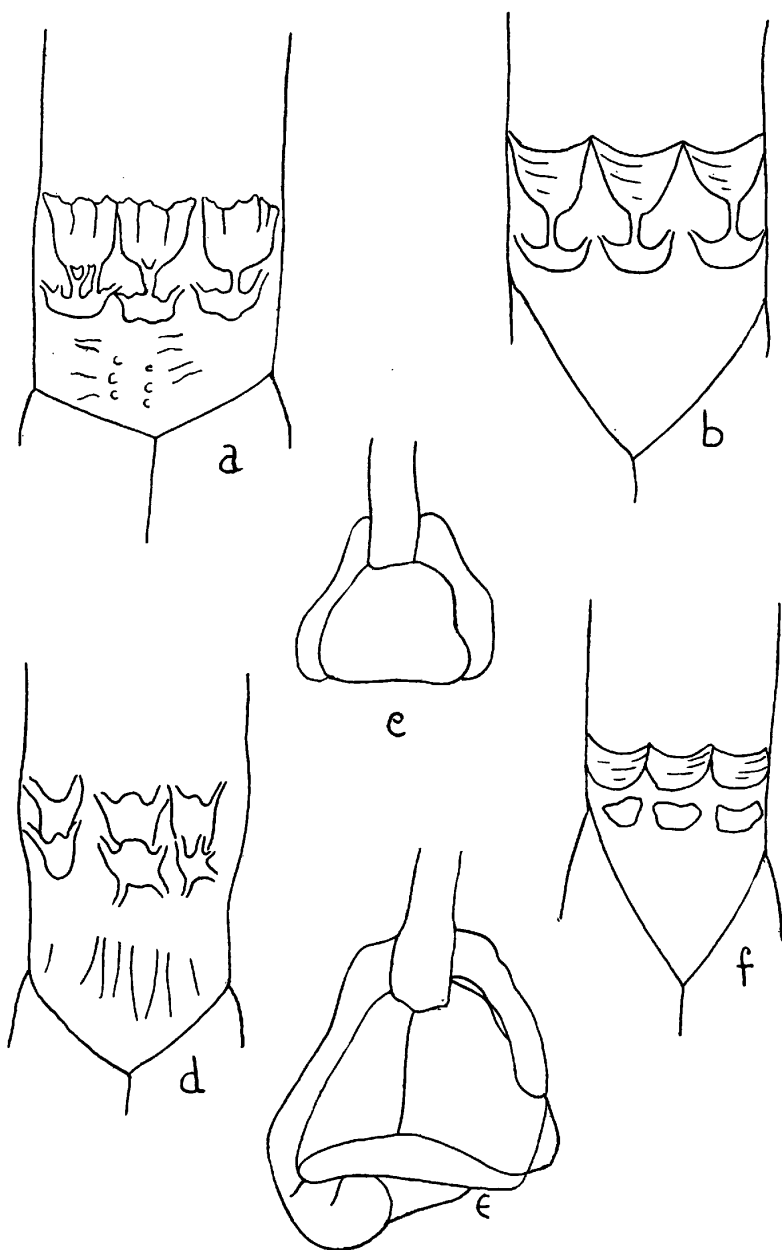


Fig. 8. Hearts and heart valves in the open conus.

a, *Halaelurus bivius*; b and c, *Atelomycterus marmoratus*; d, *Pristiurus eastmani*; e, *Halaelurus bivius*; f, *Halaelurus burgeri*.

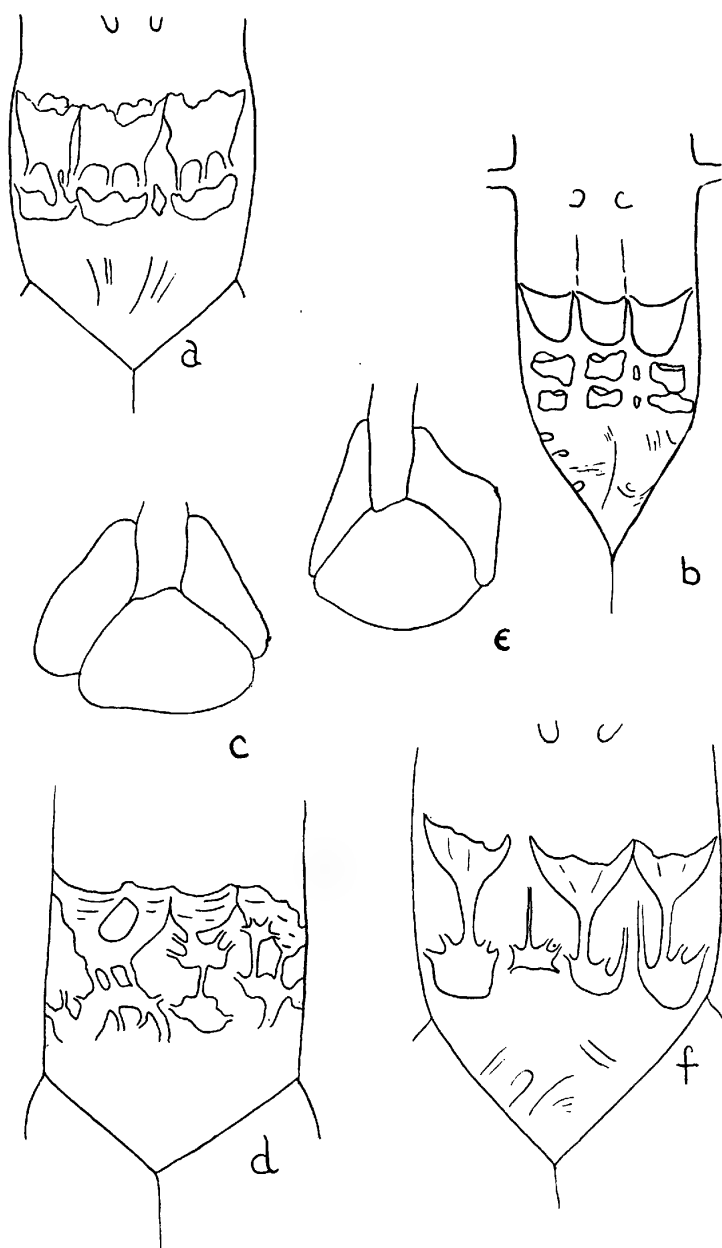


Fig. 9. Hearts and heart valves in the open conus. Note transverse duplication in process in *d*, and variation of *b* from the other members of group.

a, *Cotulus retifer*; *b*, *Calliscyllium venustum*; *c* and *d*, *Catulus torazame*; *e* and *f*, *Parmaturus xaniurus*.

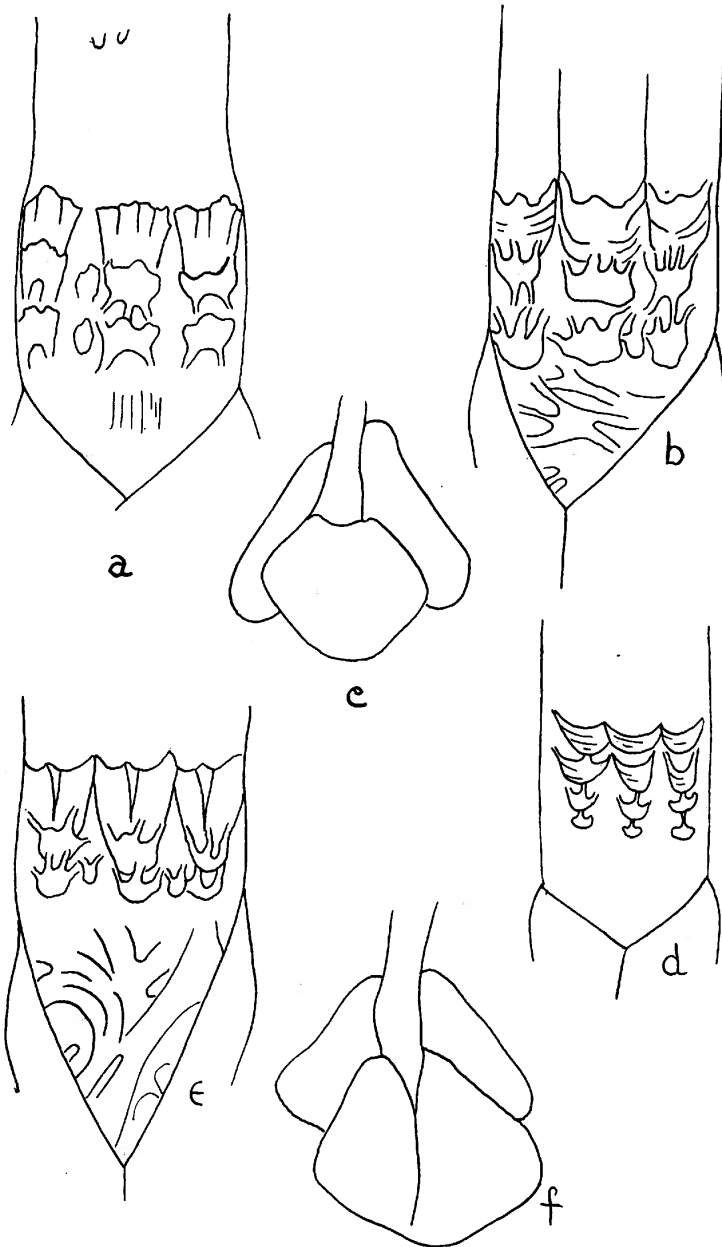


Fig. 10. Hearts and heart valves in the open conus. Note variation in *d*, and the longitudinal duplication in the other species.

a, *Galeorhinus laevis*; *b*, *Galeorhinus mustelus*; *c* and *d*, *Galeorhinus manazo*; *e*, *Galeorhinus fasciatus*.

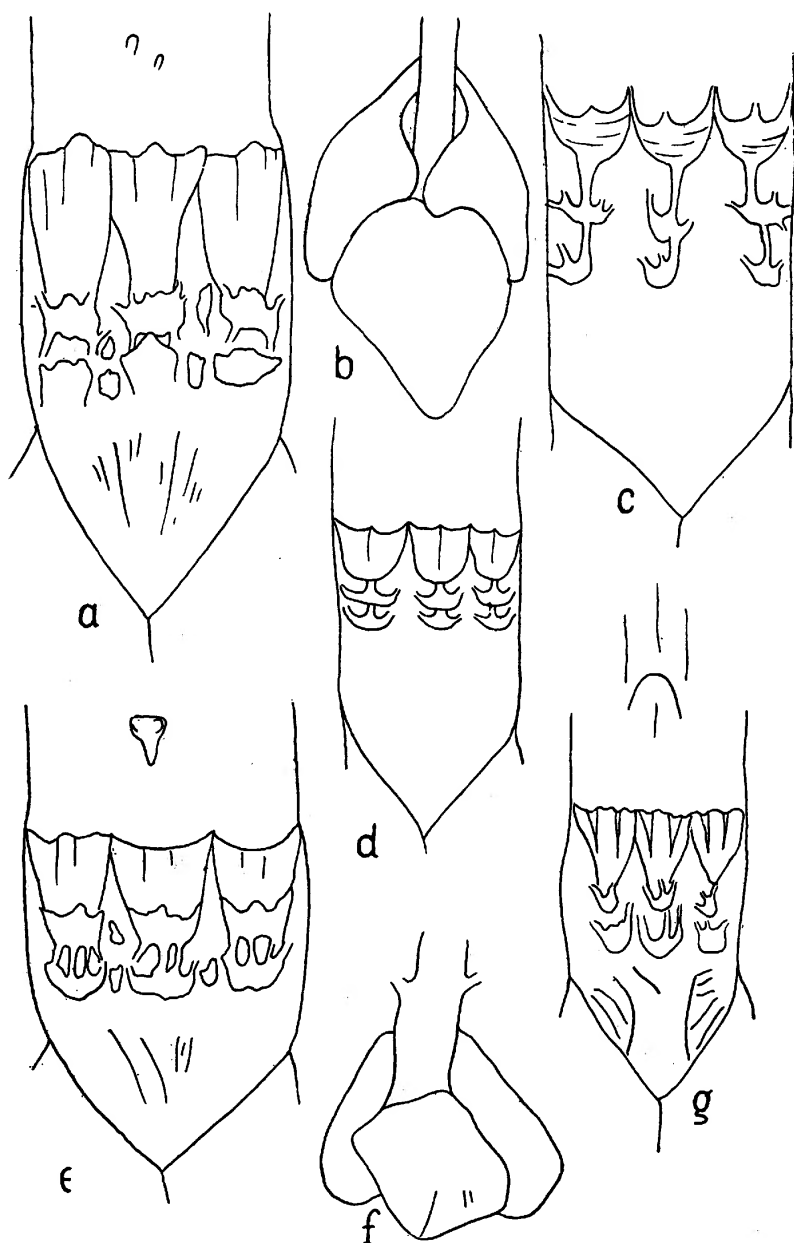


Fig. 11. Hearts and heart valves in the open conus.
a, *Carcharinus milberti*; *b*, and *c*, *Sphyrna zygaena*; *d*, *Carcharinus sorrah*;
e, *Carcharinus commersonii*; *f*, *Carcharinus sorrah*; *g*, *Sphyrna blochii*.

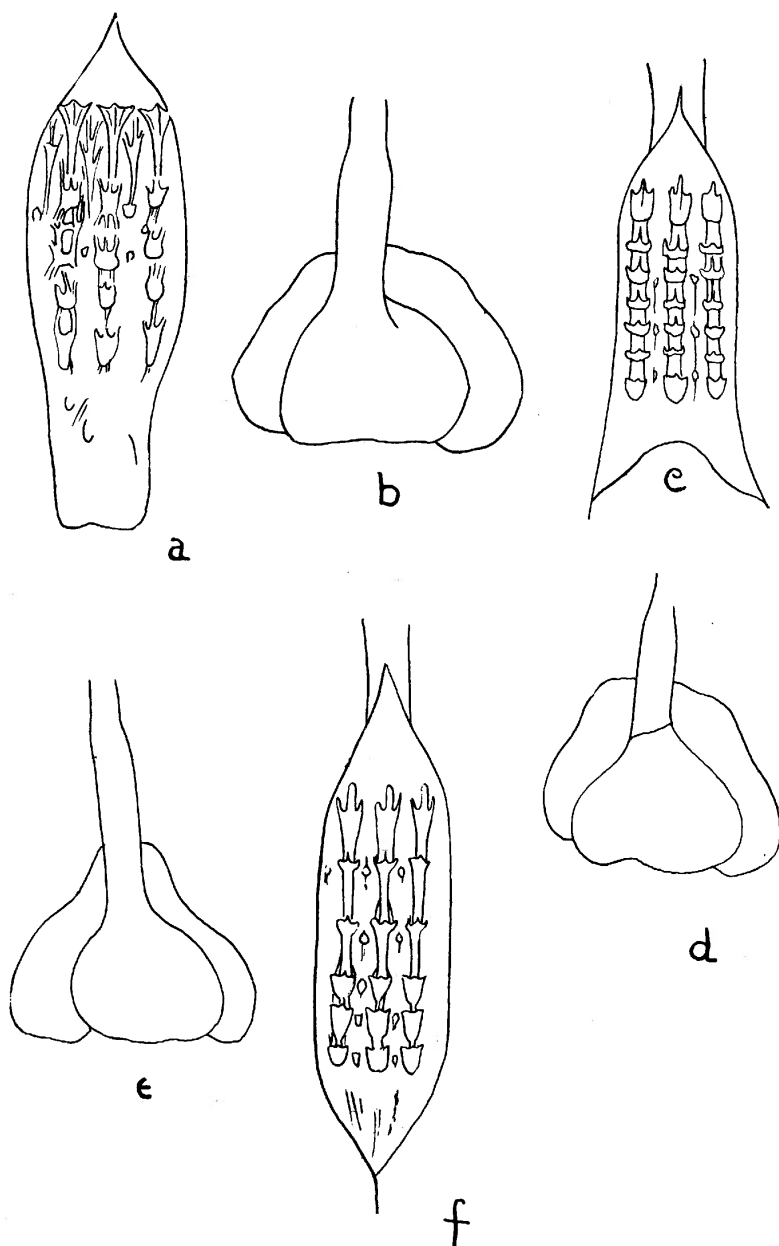


Fig. 12. Hearts and heart valves in the open conus. Note lengthening of the bulbus to accommodate the increased number of rows.

a and *b* *Aetobatus*; *c* and *d*, *Rhinoptera jussieu*; *e* and *f*, *Mobula hypostoma*.

All after Garman.

